Tree ring responses to climate variability of xerophytic thickets from South Soalara, Madagascar

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ABSTRACT

Xerophytic thickets occur along the southwestern part of Madagascar. Although providing a wide variety of resources and services to the local population, this particular vegetation is subjected to deforestation. This study focuses on linking dendroclimatology and dendroecology by examining the spatial and temporal variability of the ecological growth conditions. Information from tree rings was retrieved, on one hand, to identify the problem of the limiting effects of past climate on growth and, on the other hand, to show how local environment takes part in the growth pattern of South Soalara species, in the southwestern part of Madagascar. Methods and principles of dendrochronology were applied on nine species belonging to seven botanical families. A total of 42 stem discs from 3 to 5 trees per species were collected at 30 cm height. All discs exhibited visible tree rings, but anatomical distinctness varied between species. This study highlighted the annual formation of tree rings through successful crossdating techniques. Then, from the nine constructed chronologies, species were grouped into three clusters. Analysis between precipitation and radial growth showed that the response to climate occurred mainly in rainy season. Large-scale climatic drivers such as sea surface temperature (SST[1]) of ENSO[2] regions revealed a teleconnection with tree growth in cluster 1. Mean radial increments were computed from the measured tree ring width and varied from 0.66 to 1.98 mm year^{-1}, showing that those species are slow-growing. All species were recorded as having a certain dendrochronological potential, which was ranked as useful for *Rhizogum madagascariense* and *Terminalia gracilipes,* poor for *Gyrocarpus americanus* and problematic for the other species. It is recommended to increase the number of wood samples and to provide more knowledge on the characteristics of the species in order to improve the quality of the chronology and the climatic signal on tree rings.

1. Introduction

Natural tropical forests are incessantly threatened by global climate change and overexploitation. The degradation of natural forests through timber harvests, fuelwood collection, deforestation, expansion of agriculture, conversion to pasture, illegal logging and fires, is a major source of global greenhouse gas emissions (Pearson et al., 2017). International discussions and concerns are oriented toward a sustainable management of forest resources (Couralet et al., 2010). Several approaches and incitations related to the reduction of the emissions from deforestation and forest degradation as well as the role of conservation and sustainable forest management have been developed. The effective success of such sustainable management relies on the knowledge of the exact information on tree age, productivity and forests dynamics (Bräuning et al., 2010; Nicolini et al., 2010; Randriamalala et al., 2017). The information on specific tree growth, especially for tropical forests, is lacking, despite the growing interest toward them these days. Putz et al. (2012) gathered over a hundred publications on the sustaining values of selectively logged forest, as an alternative to the dichotomy concept of deforestation and complete preservation of tropical

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forests, and it appeared that most of the growth models derive from indirect methods based on projections and simulations as well as repeated diameter measurements of trees (Lieberman et al., 1985). Given the importance of the retrospective understanding of growth rhythm in natural forests, dendrochronology has proven its use, by providing information about tree age, species behavior, historic model reconstruction and the impact of environmental conditions during tree life span (Bräuning and Zuidema, 2005; Therrell et al., 2007).

Looking back over the last decades, annual tree-ring formation has been observed for many dry tropical trees (Worbes, 1999; Therrell et al., 2006; Rozendaal and Zuidema, 2011; Mendivelso et al., 2014). Apart from some exceptions, it is now clear that the intra-annual variability of tropical climates is closely linked to the formation of annual tree ring. Dendrochronological studies in semi-arid parts of Africa have shown the climatic and ecological importance of tree rings (Fichtler et al., 2004; Gebrekirstos et al., 2008; Wils et al., 2010; Tolera et al., 2013). However, little is known about Malagasy species dendrochronology. To our knowledge, few studies have been conducted on the dendrochronological aspects of local species. Some research projects of graduate studies have involved the determination of the anatomical and dendrochronological aspects of some genera in forests of Madagascar: *Commiphora* (Rakotoarison et al., 2012) and *Albizia* in the dry forests of Madagascar *(*Rakotoarimanga, 2012), *Tamarindus* in the gallery forest of Berenty (Raharison, 2013). The PhD thesis of Ravaomanalina (2011) in various sites showed the annual formation of tree rings of the genus *Adansonia (Baobab)*. However, none of these four studies have been published in international journals. The published works of Patrut et al. (2015, 2016) have also dated some Baobab species but did not use traditional dendrochronological techniques. None of these studies was oriented toward the characterization of the dendrochronological potential and tree ring analysis of the species from the arid region of the country.

An interesting ecosystem in Madagascar is the xerophytic thicket, consisting of a particular vegetation, in the southern part of the island (Masezamana et al., 2013). This type of vegetation is rich in endemic trees and shrub species (Razanaka, 1996), but is nonetheless suffering from deforestation. Two principal activities are to blame: slash and burn agriculture and charcoal production. To a lesser extent, there is also goat grazing (Andriaharimalala et al., 2012; Randriamalala et al., 2016). Therefore, the study of tree productivity is of primary importance for this vegetation type, if we want to know about the annual growth dynamics and the potentialities of biomass production. Furthermore, Génova et al. (2013) emphasized that studies on the growth of shrubs living in arid and semiarid environments are scarce, yet very important. This paper aims to report a new tree-ring analysis of nine species, growing in a xerophytic thicket of Madagascar and having ecological and economic interests. The ultimate objectives are to obtain basic data for the management of dry tropical forests (dendroecology) and understand the relationship between growth and local as well as large-scale climate variability (dendroclimatology).

2. Materials and methods

2.1. Site description

Wood samples were taken in the South Soalara Commune, Toliara II District, in the southwestern part of Madagascar (23° 35′ 00″ S, 43° 43′ 00″ E, 31 m; Fig. 1). This study area is characterized by a tropical semiarid dry climate with a mean annual temperature of 24.8 °C and precipitation of 350 mm characterized by two distinct seasonal distributions (Fig. 1). The wet period lasts from December to February; the remaining months are drier, with less than 60 mm per month. Those climate data were obtained from the nearest climate station, located in the Toliara Airport, 25 km from the study site (23° 23′ 00″ S, 43° 44′ 42″ E, 8 m). The main vegetation is made up of xerophytic thickets including Didiereaceae and Euphorbiaceae families, characterized by a

canopy with a height of 10 m and specific biological and physiognomic aspects, allowing an easier adaptation to the aridity of a sub-desert environment (Salomon, 1978; Razanaka, 1996). A rocky calcareous soil, some limestone and sandy soil constitute the substrate of the vegetation (Salomon, 1978; Randriamalala et al., 2016). Although the area currently maintains a low human population density, it is under intense anthropogenic influence. The main activities of the population are the breeding of small ruminants and woody charcoal production (Randriamalala et al., 2016).

2.2. Data collection, samples preparation and tree ring structure analysis

This study concerned nine species (Table 1), selected from the studied species of a former research (Randriamalala et al., 2016). Tree harvest locations (Fig. 1) were, then, derived from randomly sampled plots according to disturbance gradients and soil types (Randriamalala et al., 2016). Trees with bigger diameter were selected within each plot with the purpose of finding at least three trees per species. The species were intermixed, having grown in thickets and were essentially found in the same area, the calcareous plateau. Spiny shrubby species were individuals with a maximal height between 5 m and 7 m. On the other hand, tree species were individuals whose maximal height could reach 9 m to 11 m (Table 1). Three to five trees were harvested per species, with a total of 42 trees. Samples were collected in March 2012 and July 2013. From each tree, a cross-sectional wood disc with a thickness of 5 cm was cut at 30 cm height. Discs were air-dried. Then, their transverse surfaces were sanded with sandpaper up to grit of P800 in order to optimize growth ring detectability (Durrieu de Madron et al., 1998; Burnel and Pelissier, 2009). All stem discs were examined using an Olympus SZH10 stereomicroscope with a 7–70× magnification to carefully delineate and select two to three radii for measurement, avoiding common trunk anomalies or damages. Each ring was marked with a pencil and every fifth ring were interconnected between different radii, to check for rings continuity. Thanks to this procedure, wedging rings and discontinuous growth zones were detected and the number of errors in ring marking was reduced. Wood surfaces were scanned with a HP Scanner at a resolution of 2400 dpi. Growth ring widths were then measured to the nearest 0.01 mm by Fiji ImageJ software from bark to pith.

Wood structures of distinct growth-ring boundaries (Fig. 2) were categorized according to IAWA features (1989), adapted by Tarelkin et al. (2016), referred here as: "an abrupt structural change at the boundary, usually including change in (1) fiber wall thickness and/or (2) radial fiber diameter ». Indistinct growth rings showed « more or less gradual change in cell characteristics on a radial axis » such as (3) gradual change in radial fiber diameter, (4) gradual change in vessel diameter, (5) vessel density variation, (6) marginal parenchyma present, (7) parenchyma bands density variation and (8) distended rays. Absent rings lacked those growth-ring markers.

2.3. Statistical analysis

The discs were first visually crossdated by checking tree-ring series of all trees per species for measurement errors, then statistically crossdated by correlating the series in COFECHA which checks crossdating quality and measurement accuracy (Grissino-mayer, 2001). Individual tree-ring series were compared with one another since no reference chronology was available for Malagasy species. For standardization purposes, raw tree-ring widths were transformed into dimensionless indices with a negative linear function using ARSTAN (Cook and Holmes, 1999), and 1st order autocorrelations were removed. Tree-ring series, which showed strong correlations with one another, were selected to establish a reference chronology. To allow the representativeness of the chronology, the number of samples participating each year in the chronology was made up of at least 3 trees. Moreover, in order to increase the sample depth, a Principal
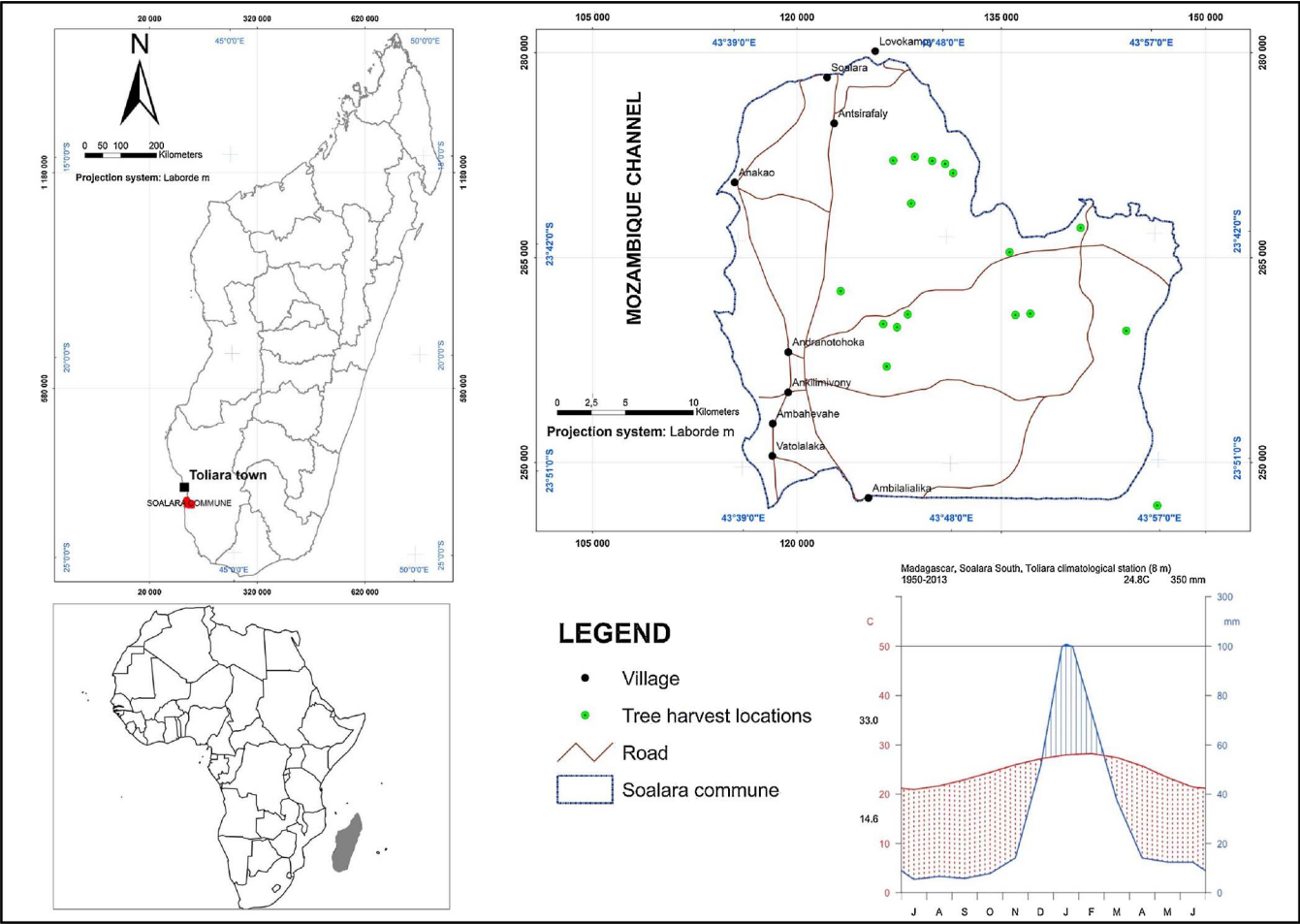
Fig. 1. Location and climate diagram of the study site (Average data for the period of 1950–2013 from Toliara station 23° 23′00″ S, 43° 43′42″ E).

Table 1
List of the nine spescies studied.

Scientific name	Common name	Family	Life form	Leafing	Flowering	Fruiting	Sources	Number of samples
Alluaudia comosa Drake	Somodradraky	DIDIERACEAE	Spiny shrub	January / December	na	na	Ratovomanana et al. (2011)	5
Cedrelopsis grevei Baillon	Katrafay dobo	MELIACEAE	Tree	January / September	October / January	November / February	Ratovomanana et al. (2011)	5
Commiphora lasiodisca H. Perrier	Vingovingo	BURSERACEAE	Tree	na	na	na		5
Gyrocarpus americanus Kubitzki	Kapaipoty	HERNANDIACEAE	Tree	December / March	September /January	October / March	Ratovomanana et al. (2011)	5
Poupartia caffra (Sond.) H. Perrier	Sakoa	ANACARDIACEAE	Tree	na	na	na		3
Rhizogum madagascariense Drake	Hazotaha	BIGNONIACEAE	Spiny shrub	January / October	November / January	February / May	Ratovomanana et al. (2011)	5
Sclerocarya birrea Hochstetter, Christian Ferdinand Friedrich	Hadim-bohitse	ANACARDIACEAE	Tree	na	na	na		4
Stereospermum euphorioides Candolle	Somontsoy	BIGNONIACEAE	Spiny shrub	na	na	na		5
Terminalia gracilipes Capuron	Fantramanty	COMBRETACEAE	Spiny shrub	na	na	na		5

Na: not available.

Component Analysis (PCA) of the ring-width index, with 77 years of common period (1938–2014), was used to identify similar modes in annual radial growth that allowed the order and classification of chronologies to be grouped into clusters. Hierarchical Clustering on Principle Components (HCPC) was also applied to indicate the number of clusters, which were chosen visually from the hierarchical tree and were based on the increase of the inertia. HCPC function makes use of Euclidean distances to define the distance between individuals, Ward's agglomeration method and 95% confidence interval to construct the hierarchical tree. The HCPC was performed with functions from package 'FactoMineR' (Husson et al., 2016).

2.4. Relationships between age and diameter

The measured annual increments of each radius of each tree and from each species were cumulated from pith to bark, doubled and
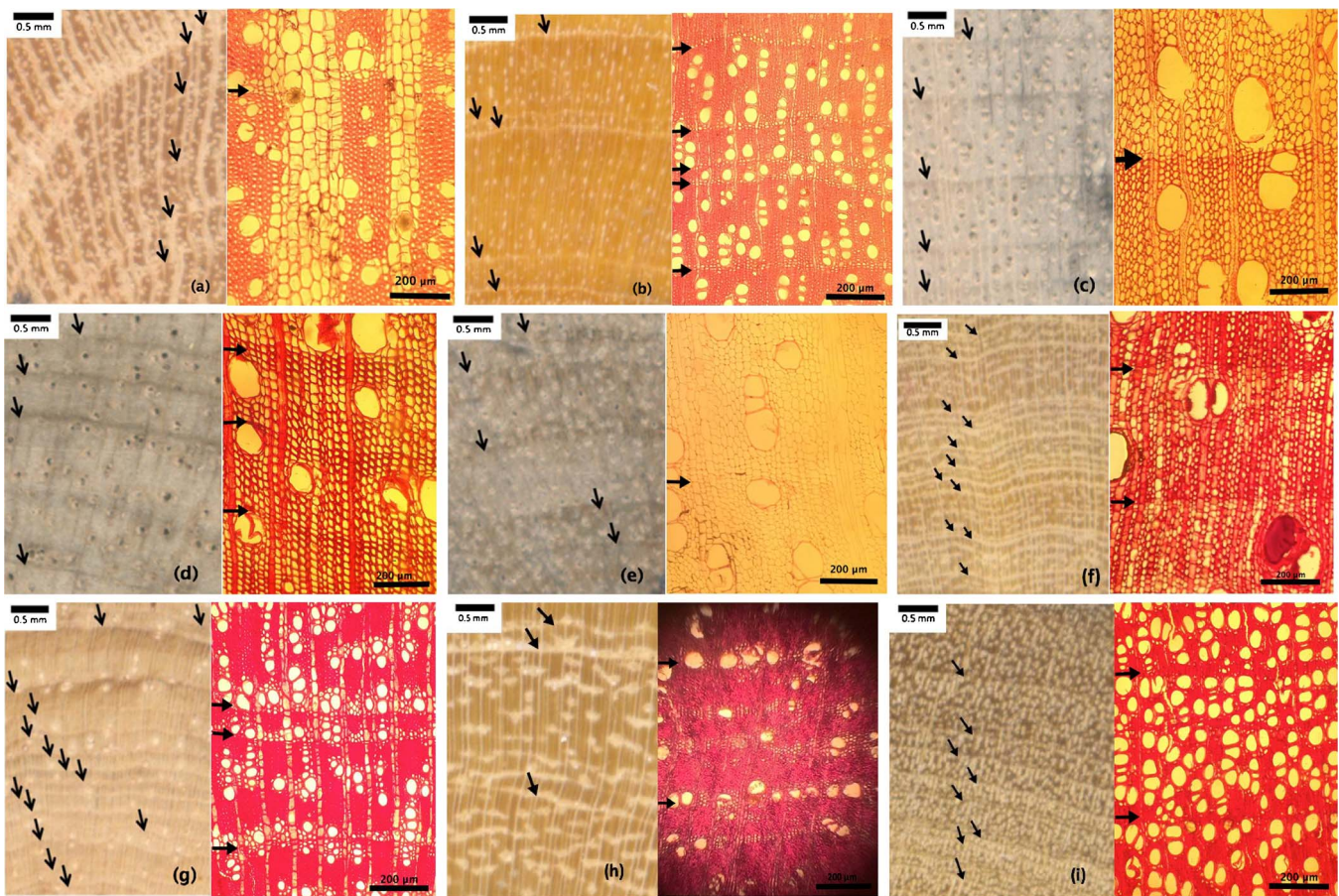
Fig. 2. Macroscopic and microscopic features of growth rings. Arrows indicate the growth boundaries. *(a) Alluaudia comosa, (b) Cedrelopsis grevei, (c) Commiphora lasiodisca, (d) Gyrocarpus americanus, (e) Poupartia caffra, (f) Rhizogum madagascariense, (g) Sclerocarya birrea, (h) Stereospermum euphorioides, (i) Terminalia gracilipes.*

averaged to construct individual cumulative diameter growth curves. To estimate the relationship between age and growth, the latter were compared to the Minimum Cutting Diameter (MCD) i.e. the minimum tree diameter size for harvesting nationally legalized in Madagascar at 10 cm for fuel wood (Order No. 13855/2001 issued by the Ministry of Environment and Forest on November 13th 2001) (MEF, 2001). According to the same law, MCD is 41.38 cm for construction wood. However, the MCD really practiced is set at 30 cm (MEF, 2013), so this last threshold was considered in this study. Linear and polynomial trend lines were used to compute the age at which trees are likely to attain the MCD.

2.5. Climate-growth analysis

At a local scale, the relationship between climate and tree growth was examined by computing the correlation coefficient between the composite chronology of each cluster and the annual, seasonal and monthly rainfall (Fritts 1976). The available precipitation time series of the nearest weather station (Toliara) were selected, which spanned from 1950 to 2013 and overlapped tree-ring chronologies. Annual rainfall was computed from June of the previous year to May of the current year. The rainy period (December-January-February), early rainy season (November-December), late rainy season (January-February), transitional period (March-April-May and September-October-November) and dry season (June-July-August) were considered as seasonal rainfall.

At a regional scale, the relation between tree growth and the SST of the equatorial Pacific and Indian Ocean was analyzed. Spatial correlation maps were extracted from KNMI Climate Explorer (Trouet and Van oldenborgh, 2013) from HadISST1 datasets between 1996 and 2014

(Rayner et al., 2003) based on 1°x1° monthly fields for clusters with a significant positive correlation with climate. The SST indices for the Niño 3.4 regions were used to assess the association with Niño events (Trenberth, 1997). Correlations between precipitation and tree growth were calculated for the same species and over the same time span of instrumental climate data. Spatial correlation maps were generated based on gridded 0.5° × 0.5° monthly precipitation fields with CRU TS3.23 datasets (Harris and Jones, 2015), to indicate which oceanic regions were most related to precipitation and tree growth patterns ($p < 0.10$).

2.6. Dendrochronological potential

The dendrochronological potential was determined for each species using the system elaborated by Tarhule and Hughes (2002) and also used by David et al. (2014), which attributes three categories to the species: useful, problematic and poor. Each studied species was analyzed through the following five criteria: tree-ring distinction, cross-dating, circuit uniformity, tree-ring anomalies and tree-ring width variability (sensitivity). A sixth criterion indicated as "precipitation influence on growth" was also taken into account.

Species were classified as "potentially useful" when (a) they exhibited distinct tree ring that can be identified and measured; (b) Crossdating can be done successfully, at least for certain samples; (c) tree rings were generally consistent through the entire section; (d) anomalies were minimal or absent; (e) tree rings were variable indicating (f) there is a possible relationship with climate. The « problematic » category referred to species satisfying some criteria, but a great care is needed to detect tree ring. Finally, when the application of standard dendrochronology methods didn't improve the identification

of tree rings, the potential was set as « poor ».

3. Results

3.1. Microscopic and macroscopic characteristics of growth rings

The distinctness of rings varied between the nine species studied and each tree (Fig. 2) but was always sufficiently clear to mark individual rings on woody stems. The visibility depended on the ring width: wide rings were generally distinct, but distinctness decreased following the decrease in ring widths, for instance, towards the center of the tree. Indistinct ring boundaries were macroscopically represented by darker bands, so ring widths were measured from the beginning of those bands to the beginning of the bands of the next ring.

The presence of marginal parenchyma bands showing distinct growth rings were discriminated in some species: *A. comosa* (Fig. 2a), *C. grevei* (Fig. 2b), *R. madagascariense* (Fig. 2f), *S. birrea* (Fig. 2g) and *S. euphorioides* (Fig. 2h).

The growth rings of *C. grevei* (Fig. 2b) were discerned by an abrupt change in the radial fiber diameter. Ring boundaries of *C. lasiodisca* (Fig. 2c) and *G. americanus* (Fig. 2d) were distinguished by an additional features: an abrupt change in fiber wall thickness. A gradual change in the radial fiber diameter indicating distinct growth rings was displayed by *C. lasiodisca* (Fig. 2c), *G. americanus* (Fig. 2d) and *R. madagascariense* boundaries (Fig. 2f). *T. gracilipes* (Fig. 2i) and *S. birrea* (Fig. 2g) growth rings were distinct and identified by a variation of the vessel density. Indistinct ring boundaries of *P. caffra* (Fig. 2e) were delineated by a gradual change in radial fiber thickness. A slight decrease in the vessel diameter allowed the delineation of *P. caffra* (Fig. 2e) and also of *R. madagascariense* (Fig. 2f).

The wood of all species was diffuse-porous. Some individuals showed large differences in growth rates between radii with asymmetric centers. Problems relating to tree-ring identification occurred for shorter radii, where several wedging rings were present. Visual cross dating between different radii solved this issue. Vague bands disappearing along one of the radii were considered to be intra-annual growth variations, and thus, no true ring boundaries were present (De Micco et al., 2016). These intra-annual variations vary between species depending on their specific wood anatomy consisting of bands of thick-walled fibers or discontinuous parenchyma bands (Groenendijk et al., 2014).

3.2. Tree-ring measurements and chronology development

Usual secondary growth anomalies of shrubs (asymmetric, lobbed and eccentric pith axes) were observed in some samples, and some of the older ones presented heart rot. Eighty-six out of 117 growth series were measured, synchronized and averaged into nine species chronologies (Table 2; Fig. 4). All nine chronologies had extremely high year-to-year variability and common signal as indicated by the high values of the mean sensitivity (0.46–0.86). The nine species also showed a wide variety of mean sensitivity: *R. madagascariense* (0.86) is the most affected by climate variability while *Gyrocarpus americanus* (0.46) is less sensitive. Those values are superior to 0.2 suggested by Speer (2010), which implies that tree growth in South Soalara is influenced by an environmental factor. The autocorrelation value varied between 0.064 (*R. madagascariense*) and 0.51 (*C. lasiodisca*). Values higher than 0.5 correspond to a great influence of the previous year on growth. *R. madagascariense* showed a high value of mean sensitivity coupled with low value of autocorrelations. Series intercorrelation, whose strength varies between species, is an important parameter to assess the quality of the chronology. *A. comosa* (0.46), *S. euphorioides* (0.44), *S. birrea* (0.41), *T. gracilipes* (0.41) and *P. caffra* (0.36) showed medium to high correlations (with p < 0.1) between tree-ring series of different trees, while the correlations for the other species were considerably lower. For the aforementioned species, the site is homogeneous while for the others, the climatic signal intensity is less obvious. The Expressed Population Signal ranged from 0.63 (*C. grevei* and *P. caffra*) to 0.81 (*A. comosa*), indicates that trees are coherent in growth but that the statistical quality of the mean site chronology is weak compared to an infinitely replicated chronology. The studied species showed an EPS lower than the threshold 0.85 considered for chronology's reliability, which is probably explained by the low number of samples (Wigley et al., 1984). However, *A. comosa* and *S. euphorioides* showed values higher than 0.80, the threshold that could be used for tropical species (Mendivelso et al., 2014).

The PCA between tree ring chronologies explained 56.63% of the total variability (Fig. 5). There are three main clusters for the period 1996–2012, cluster 1: *A. comosa, R. madagascariense, T. gracilipes, C. lasiodisca, G. americanus* and *P. caffra*, cluster 2: *C. grevei* and *S. birrea*, and cluster 3: *S. euphorioides*. Those overall results show that trees of the same species synchronize their growth in response to a common environmental factor. Species grouped in each cluster then show similar growth pattern.

3.3. Relationship between age and diameter

Longevity differences were observed between species. Mean ring widths of all studied species were less than 1 mm corresponding to a mean radial growth of less than 2 mm per year. Mean ring widths ranged from 0.66 mm per year for *R. madagascariense* to 1.98 mm per year for *A. comosa* and *S. euphorioides* (Table 3). Mean cumulative diameters varied from 3.60 cm for *S. euphorioides* at the age of 16, to 16 cm for *C. lasiodisca* at the age of 78 (Table 3). Indeed, it will take *S. birrea* at least 122 years to reach the legal Minimum Cutting Diameter of 10 cm and 335 years to reach the 30 cm MCD. Even for *A. comosa*, which is supposed to grow faster than the other species, it will take not less than 48 years to reach the 10 cm MCD and 117 years for 30 cm (Fig. 3, Table 3).

Table 2

Characteristics of the first reference chronologies in Southwestern of Madagascar.

Species	Series	SI	MS	AC	MRW ± SD	RP (Age)	EPS	% Absent rings	DP
Alluaudia comosa	5 (8)	0.46	0.54	0.28	0.99 ± 0.68	1976–2012 (36)	0.81	4.5	Problematic
Cedrelopsis grevei	5 (10)	0.25	0.66	0.32	0.42 ± 0.33	1945–2012 (67)	0.63	7.3	Problematic
Commiphora lasiodisca	5 (10)	0.28	0.51	0.51	0.96 ± 0.51	1933–2011 (78)	0.66	4.4	Problematic
Gyrocarpus americanus	5 (8)	0.31	0.46	0.29	0.87 ± 0.56	1947–2011 (65)	0.69	1.1	Poor
Poupartia caffra	3 (7)	0.36	0.68	0.15	0.87 ± 0.66	1987–2010 (23)	0.63	7.5	Problematic
Rhizogum madagascariense	5 (11)	0.30	0.86	0.064	0.33 ± 0.29	1937–2012 (75)	0.68	9.8	Potentially useful
Sclerocarya birrea	4 (8)	0.41	0.67	0.13	0.40 ± 0.28	1968–2012 (44)	0.74	6.4	Problematic
Stereospermum euphorioides	5(12)	0.44	0.65	0.153	0.99 ± 0.72	1996–2012 (16)	0.80	3.1	Problematic
Terminalia gracilipes	5(12)	0.41	0.64	0.30	0.60 ± 0.39	1974–2012 (38)	0.78	7.0	Potentially useful

SI = Mean Series Intercorrelation, MS = Mean Sensitivity, AC = Autocorrelation, MRW = Mean Ring Width, SD = Standard Deviation, RP = Record Period, EPS = Expressed Population Signal, DP = Dendrochronological Potential.
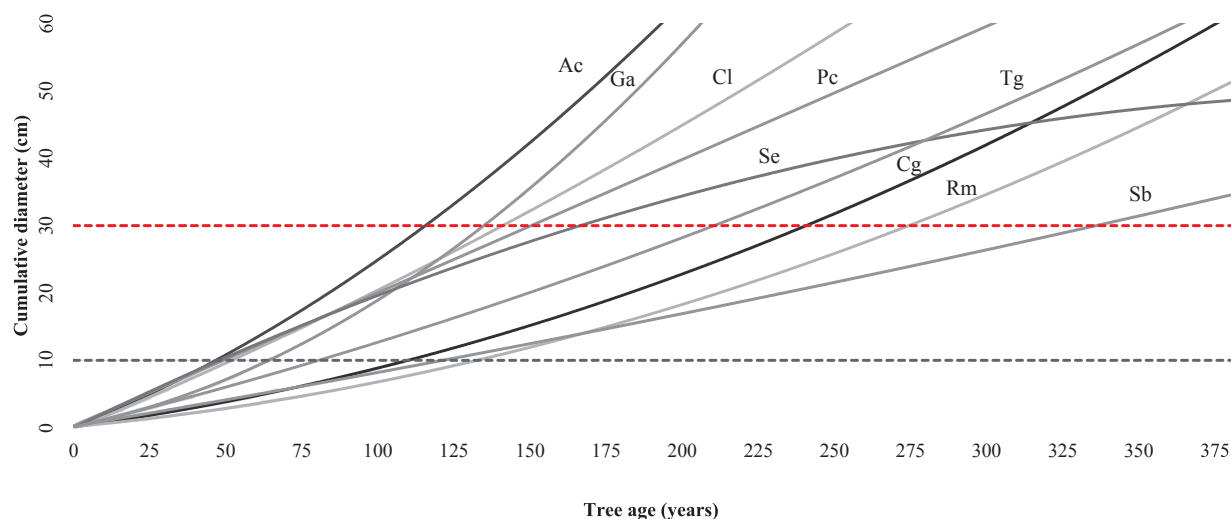
Fig. 3. Radial growth trends of nine species to reach minimum cutting diameter. *Ac = Alluaudia comosa, Cg = Cedrelopsis grevei, Cl = Commiphora lasiodisca, Ga = Gyrocarpus americanus, Pc = Poupartia caffra, Rm = Rhizogum madagascariense, Sb = Slerocarya birrea, Se = Stereospermum euphorioides, Tg = Terminalia gracilipes.* Dotted red line: minimum diameter cutting limit of 10 cm for fuel wood, dotted purple line: minimum cutting diameter of 30 cm for construction wood. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.4. Relationship between growth and climate

At a local scale, no significant correlation was found between the growth of each cluster and the total annual precipitation. However, when months are taken individually or grouped per season, it showed influence on growth, which varies widely between the three groups of species (Fig. 6). Cluster 1 showed a strong correlation with the monthly rainfall of October ($r = 0.58$, $p < 0.05$) and seasonal rainfall of the early wet season at the beginning of the current growing season (SON, NDJ; all $r > 0.48$, $p < 0.05$). However, we observed that cluster 2 correlated negatively with the wet season (DJF, $r = -0.56$, $p < 0.05$). Cluster 3 was also correlated negatively with August rainfall (DJF, $r = -0.49$, $p < 0.05$) (Fig. 6).

At a regional scale, Fig. 7 shows a spatial correlation between reconstructed precipitation from CRU TS3.23 time series and the cluster most sensitive to rainfall, which verifies the correlations of Fig. 6 (Cluster 1). Ring width chronology showed a high correlation between October rainfall in Southern Madagascar and South Africa (Fig. 7a). For the grouped months, the association between November to January rainfall and tree growth of six species of cluster 1 was observed exactly in the study area.

The cluster which is the most sensitive to rainfall (cluster 1), showed a dipole response with sea surface temperatures (SSTs) of South Atlantic Ocean, being positive for the region Equator −30°S and negative for the region below 30°S, during October (Transitional period to the rainy season). Regarding the Tropical Atlantic SSTs, a partial negative correlation between cluster 1 chronology with Niño 3.4 region and below 30°S was observed during November to January (rainy months) (Fig. 8).

Concerning the dendrochronoloical potential of each species, summarized in Table 2, *R. madagascariense* and *T. gracilipes* were listed as being "potentially useful", G. americanus as "poor" and the other species as "problematic".

4. Discussion

4.1. Tree-ring formation

The anatomical description of microscopic and macroscopic features of the species tree ring were made, and visible rings allowed their measurement. Thanks to the successful crossdating of each series and an influence of climate over growth, a dendrochronological assessment can be made on the nine species. To the knowledge of the authors, the wood anatomy of two of the studied species (*P. caffra* and *T. gracilipes*) was investigated for the first time in this study. Among the nine studied species, only the dendrochronology of *S. birrea* was previously studied by Gebrekirstos et al. (2011), in order to explore climatic signals in this species tree ring in West Africa. Also, no previous dendrochronological potential researches were conducted on the other eight species. Those constitute a novelty for this study.

All nine species exhibited growth rings, but it was sometimes difficult to distinguish them because of the slow growth of the tree. Moreover, substantial differences in distinctness among species were encountered. This is probably due to a species-specific wood structure (Détienne, 1989). Terminal parenchyma bands were the clearest marks to macroscopically distinguish tree ring boundaries, while microscopically, an abrupt change in fiber wall thickness and in radial fiber diameter marked distinct growth rings. Nevertheless, Tarelkin et al. (2016) underlined that the diversity of growth rings should be acknowledged without being limited to distinct, indistinct or absent. Even if some feature were indistinct, it is important to highlight that the identification and measurement of individual rings were possible.

As a common problem in many dendrochronological studies of tropical species (Trouet et al., 2010; De Ridder et al., 2013b), as well as in tree ring formation of thicket species in Madagascar, anomalies, mostly wedging rings, which are assumed to be associated with phases of low growth rates and eccentric growth, hampered the analysis. Wils et al. (2010) outlined that tree growing in difficult conditions are more prone to develop multiple missing rings. However, less ring measurement mistakes were made by checking the continuity of rings over the entire stem disc. Bräuning and Zuidema (2005) emphasized the absolute necessity of working with a whole stem disc and checking the continuity of rings whilst studying with new tropical species. Tree-ring detection on the pith was also problematic due to the wood structure in this zone, especially since the samples were collected at the base of the stem. This inconvenience could have been avoided if the discs were collected at breast height, but trees real age would not have been estimated properly (Lopez et al., 2005). Finally, the lack of long-climatic data records also limited the study.

4.2. Master chronology characteristics

The establishment of the tree-ring chronologies was carried out with relatively high inter-series correlations. The success of crossdating
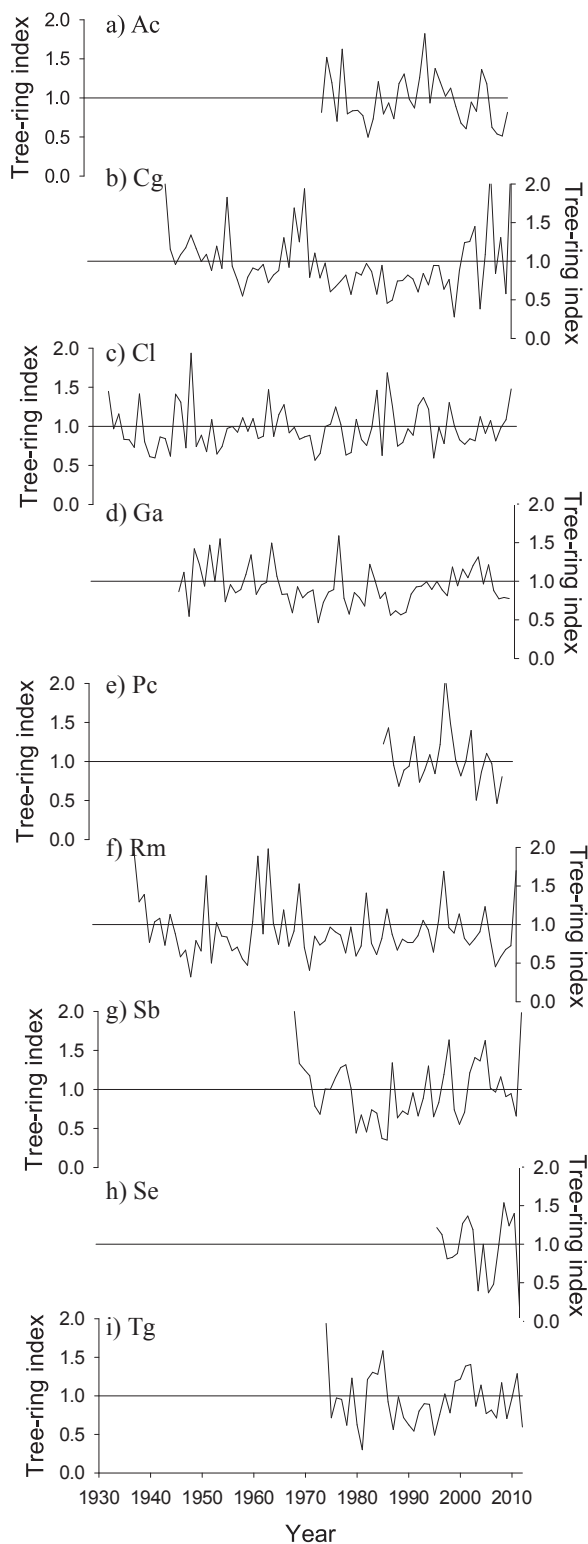
Fig. 4. Tree ring chronologies of the nine study species of Soalara South. *Ac = Alluaudia comosa, Cg = Cedrelopsis grevei, Cl = Commiphora lasiodisca, Ga = Gyrocarpus americanus, Pc = Poupartia caffra, Rm = Rhizogum madagascariense, Sb = Sclerocarya birrea, Se = Stereospermum euphorioides, Tg = Terminalia gracilipes.*

Fig. 5. Individual factor map of the first two principal components of the analysis of nine tree rings chronologies. The first (Dim 1 axis) and second (Dim 2 axis) principal components are represented, which indicate how much variation is explained by the principal components. Colors represent 95% confidence intervals of population groupings.

found similar (Gazol and Camarero, 2012; Lopez et al., 2005) and higher (Stahle et al., 1999; Therrell et al., 2006 Nicolini et al., 2010) series intercorrelation values compared to the species from Soalara. EPS values of Soalara species were similar to the findings of Gazol and Camarero (2012), but weaker than the threshold 0.85 suggested by Wigley et al. (1984) and those of other findings (Lopez et al., 2005; Nicolini et al., 2010; De Ridder et al., 2013a). The mean sensitivity values of South Soalara species remain in the amplitude of those found by Lopez et al. (2005) but are higher than the mean sensitivity in other studies (Fichtler et al., 2004; Nicolini et al., 2010; De Ridder et al., 2013a). A series intercorrelation of about 0.4 is considered crossdatable, but this value is relative because it varies widely among species and region (Fritts, 1976). Lower parameter values at our study site could be explained, first by the absence of master chronology in Madagascar, secondly by the probable existence of multiple measurement errors, and above all by the limited number of samples allowing the site representativeness of tree growth (Therrell et al., 2006). However, visual crossdating was crucial for the tree-ring analysis of the nine species as also for all tropical species (Trouet et al., 2010; De Ridder et al., 2013b) because the intertree and interseries correlations are usually rather low in tropical forests according to De Ridder et al. (2014).

4.3. Relationship between age and diameter

The annual radial increments of Soalara species were comparable to those of other species growing in arid or semi-arid environments (Gebrekirstos et al., 2008; Lopez et al., 2005), but lower compared to those of other species (Nicolini et al., 2010; De Ridder et al., 2013a; Gazol and Camarero, 2012). In general, Soalara species are slow-growing species. Most chronologies from those aforementioned study areas extended between 15 and 140 years. For Soalara species, tree age of more than 50 years is already remarkable for slow-growing species and for sites were logging is frequent. Defined MCDs are used for some species categories, not derived from scientific data, but rather obtained from estimations and/or legal restrictions. In order to inhibit over-exploitation and to respect slow growth rate, the MCD should consider the ontogenetic growth and should be measured locally due to site-specific conditions (Schöngart et al., 2007; Therrell et al., 2007). The growth trend curves show discrepancies in comparison with the currently practiced forest management criterion (MCD of 30 cm). Trees will not reach a diameter of 30 cm until hundreds of years. This MCD is thus inappropriate and inefficient for the management of the timber resources of the slow-growing species.

between individuals of the same species proves that a similar variation in their growth pattern is not a coincidence (Stahle, 1999), and that an external factor influences in the same way, tree growth corresponding to a periodical wood formation (Eckstein et al., 1981; Worbes, 1995).

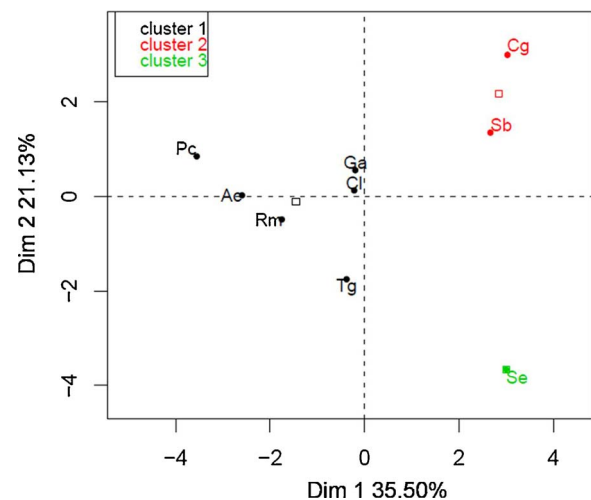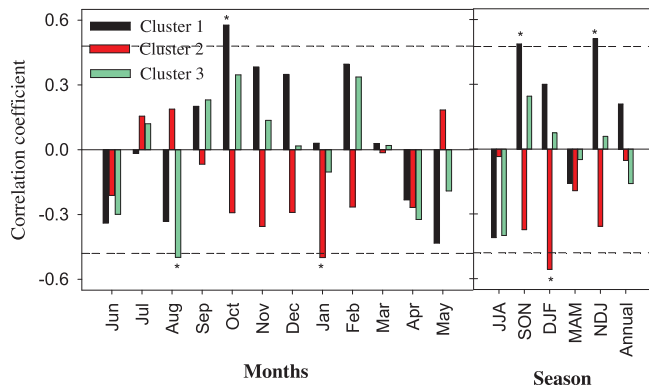Several authors working with species from arid and semi-arid areas

Table 3
Growth characteristics of the study species.

Species	Age (years)	Annual diameter increment (mm year⁻¹)	Cumulative diameter (cm)	Age to reach 100 mm diameter (years)	Age to reach 300 mm diameter (years)
Alluaudia comosa	36	1.98	70	48	117
Cedrelopsis grevei	67	0.84	56.4	111	243
Commiphora lasiodisca	78	1.92	160	53	142
Gyrocarpus americanus	65	1.74	104.3	65	136
Poupartia caffra	23	1.74	54.9	50	151
Rhizogum madagascariense	75	0.66	47.1	134	277
Sclerocarya birrea	44	0.8	37.8	122	335
Stereospermum euphorioides	16	1.98	36	49	168
Terminalia gracilipes	38	1.2	45.7	81	211

Fig. 6. Correlations between tree ring chronology (clusters) and total rainfall, during common period (1996–2012) by months and seasons. Left graphics indicate the correlation for months and right graphics indicate the correlation for season (JJA: June to August; SON: September to November; DJF: December to February; MAM: March to May; ND: November to December (begin of growth season); NDJ: November to January (first three months of heavy rains); annual: total annual rainfall. Horizontal lines and asterisks indicate statistical significance at 95% confidence level (p < 0.05).
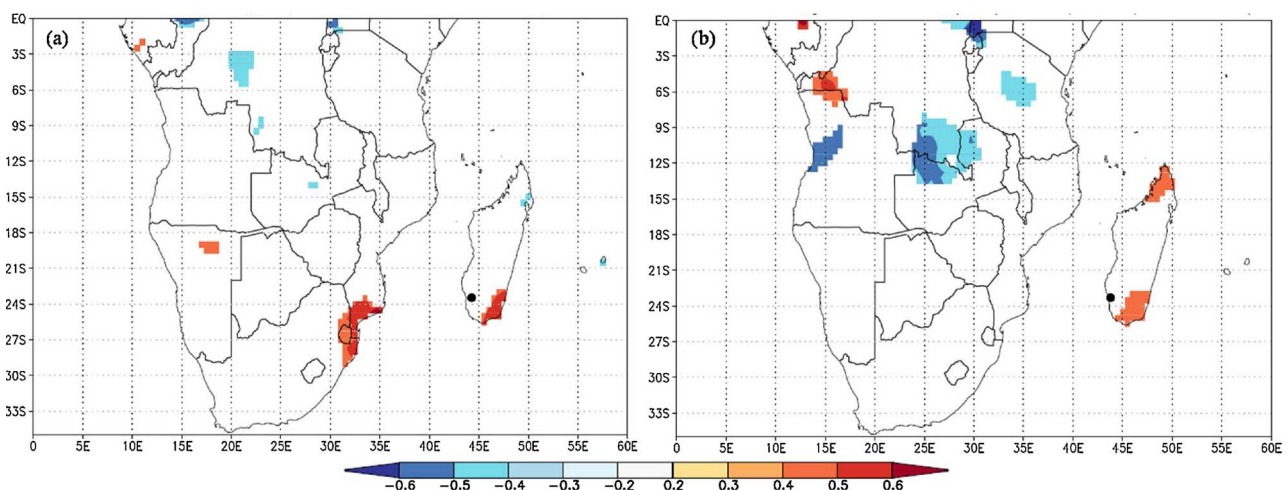
4.4. Climate/growth relationship

Precipitation in the southwestern part of Madagascar did not show any changing trend for the periods of 1929–1995 and 1999–2010 but showed an interannual variability (Rasamimanana et al., 2012). However, five extreme events occurred during these periods: two droughts (1936–1937 and 1991–1992) and flooding in three wet seasons (1953–1954, 2004–2005, and 2010–2011), which could have influenced the growth of water dependent species from cluster 1 (*A. comosa, R. madagascariense, T. gracilipes, C. lasiodisca, G. americanus* and *P. caffra*), whose relations with rainfall were positive. The rainfall regime was highly variable, but there were no long-term directional trends in precipitation (Rasamimanana et al., 2012).

The crucial moment of the growing season in dry tropical forests usually corresponds to the rainy periods (Worbes, 1999). Indeed, for all three clusters and according to the available data, the onset of leaf expansion was at the core of the rainy season (December-January; Table 1). Thus, their growth was constrained by water availability (Mendivelso et al., 2014).

One possible explanation of our results might be that, during transitional periods between dry season and rainy season, precipitation triggers the initiation of cambial activity and bud dormancy breakage in deciduous species (Dünisch et al., 2003; Bräuning and Zuidema, 2005), while at the beginning of the rainy season, rainfall determines tree ring width (Dünisch et al., 2003; Fichtler et al., 2004) and has a significant impact on tree growth diameter (Worbes, 1999; Bräuning and Zuidema, 2005).

The interannual variation of rainfall during and around wet periods might explain the onset or the delay in tree response (Couralet et al., 2010). Leaf shedding happens mostly at the beginning of the dry season (March) for taller trees and at the transitional period to wet seasons (September-October) or later for spiny shrubs. In fact, trees adopt different water-use strategy, according to species-specific physiology and phenology, which are closely related to seasonal soil hydric status and water retention capacity (Borchert, 1999; Mendivelso et al., 2014). Deciduous species lose their leaves when water is no longer available (Gebrekirstos, 2006), and then enter into cambial dormancy, implying the formation of tree rings (Borchert, 1999; Worbes, 1999).

Fig. 7. Spatial correlation between tree ring chronology from cluster 1 and precipitation (CRU TS3.23) for the period of 1996–2014 by KNMI Climate Explorer. (a) Monthly rainfall of October. (b) Seasonal rainfall of November to January. Colored areas are statistically significant at 90%. Values on the color scale correspond to the correlation coefficients (P < 0.1, r ~ 0.40). Black circle indicates study area (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).
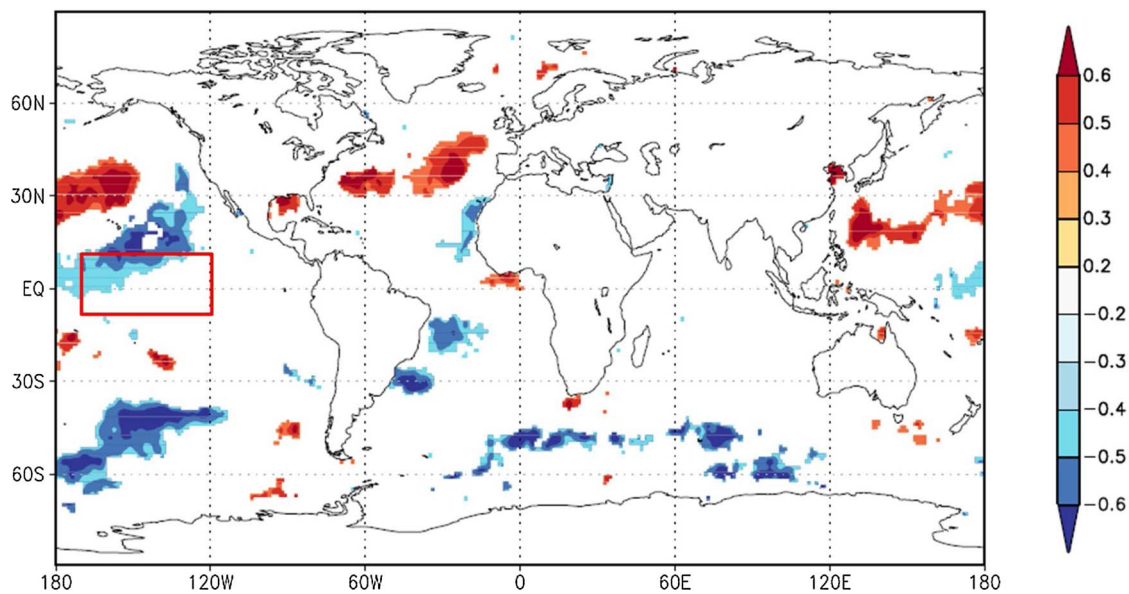
Fig. 8. Spatial correlation between tree ring chronology from cluster 1 and sea surface temperature (HadISST 1 reconstruction 1.0° × 1.0°) from November to January. Colored areas are statistically significant at 90% (Significant connection in the map (p field < 20.0%)). Niño 3.4 region is indicated by a red rectangle. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

Opportunistic species benefit from infiltrated water long after rainfall occurs thanks to their deep roots and their trunks (Borchert, 1994a). However, negative correlations during rainiest month for cluster 2 might be explained by the fact that some tropical species have a negative association with rainfall during the wet season due to water saturation in the soil (Venegas-González et al., 2016).

Studies under comparable precipitation levels showed that tree growth was influenced by rainfall within the same correlation value as in South Soalara: Tsimanampetsotsa Park in Madagascar (Ratovomanana et al., 2011), Andohahela Park in Madagascar (Andriaharimalala et al., 2012), Bezà Mahafaly in Madagascar (Rasamimanana et al., 2012) and in the semiarid forests in Namibia (Fichtler et al., 2004). Other researchers discovered higher correlation at 5% level, with sample size of at least five trees per species: in the arid and semi-arid tropical lands of Latin America (Enquist and Leffler, 2001; Lopez et al., 2005; Pagotto et al., 2015); in the Keita Valley of Niger (Nicolini et al., 2010); in the semi-arid tropics of Africa (Gebrekirstos et al., 2008). On a nearer site, in Tsimanampetsotsa National Park, Ratovomanana et al. (2011) found out that within a given vegetation formation, deciduous species did not react similarly to environmental factors and the loss of leaves was asynchronous among different species within the same family. In the same perspective, for species growing in xerophytic thickets of Bezà Mahafaly and Betioky, leafing is narrowly influenced by precipitation and drier periods are marked by leave drop (Andriaharimalala et al., 2012). The data from this study confirmed earlier observations (Ratovomanana et al., 2011) that *R. madagascariense* reacts considerably to climate variability, while *G. americanus* is less affected by climatic variation. Among abiotic factors, water availability is the most important even though the conditions that plants perceive as a drought can vary in relation to temperature, humidity, and the availability of water in the soil (Andriaharimalala et al., 2012). Rasamimanana et al. (2012) suggested that rainfall is used immediately for tree growth while underground water is used only during hydric stress.

Rainy seasons coincide with ENSO peaks of amplitudes and the effects on precipitation variability are felt in the southern part of Africa (Camberlin et al., 2001). Nevertheless, the influence of the hot phase (El Niño) on climate is a decrease in precipitation. On the opposite, La Niña phase causes an increase in precipitation (Nicholson and Entekhabi, 1986). This was partially verified in cluster 1 at the rainy

period (Fig. 8). Indeed, even if wet conditions were reported by Dunham et al. (2010) to occur during El Niño in Madagascar, certain regions of the island experiment drought. Furthermore, ENSO substantially influences the daily frequency of rainfall in the South West of Madagascar (Valimba et al., 2016; Randriamahefasoa and Reason, 2016). Mason and Jury (1997) reported that SSTs higher than normal (El Niño) are associated with drier months and SSTs lower than normal (La Niña) are linked with wet months. Nonetheless, a shift of phase is observed between the East of South Africa and Madagascar in the Indian Ocean (Jury et al., 1995). Precipitation responds to SST subtropical dipole, suggesting that when SSTs are hotter than normal in the South of Madagascar and cooler in the western part of Australia (Reason, 2001), an increase in precipitation is observed in many regions of southern Africa. Those processes play an equivalent role as ENSO on precipitation. The existence of this structure accounts for almost 12% on the variability of the Indian Ocean SSTs and contributes to severe climatic anomalies, which can hide the actions of ENSO (Ingram and Dawson, 2005). However, no significant spatial correlation was found in the Indian Ocean, which can be attributed to bias of clustering and low replications. Moreover, SSTs in the central South Atlantic Ocean is associated with rainfall in southern African regions (Mason, 1995) and Madagascar (Reason, 2001), which is verified in the results (Fig. 8). Therefore, an increase of SSTs in October is indirectly related to tree growth of species of cluster 1.

Nevertheless, the lack of repetitions from the samples leading to a weaker value of some statistics, prevents us from furtherly discussing this aspect of large climatic drivers. Hence, studies about precipitation and teleconnections with global climate (e.g. ENSO, Indian Ocean index, etc) based on tree species from cluster 1 are recommended, but it is necessary to increase the number of samples. But, the novelty of the study and the fact that it is one of the rare dendrochronological studies in Madagascar, constitute the importance of this research.

4.5. Annual tree ring formation

Evidences indicate that the delimited tree rings are annual. One the one hand, there is a clear demarcation between dry and wet season. The study site has 9 months of dry season. Meteorological conditions are wet enough to allow growth during rainy seasons and dry enough to substantially delay or entirely stop the growth during the dry season.

Besides, the studied species are deciduous (Ratovomanana et al., 2011; Andriaharimalala et al., 2012; Rasamimanana et al., 2012). The phenology, in response to this external factor (water deficit), induces cambial dormancy and allows tree-ring formation. However, little is known about tropical species phenology (Borchert, 1994a) in general and for the studied species phenology in particular.

On the other hand, the annual pattern is confirmed by series successful crossdating. Indeed, the existence of synchronized wood formations between different trees is a strong indication that their growth is linked to a factor of annual cycle (Stahle et al., 1999; Worbes, 1995). The correlation computed between the nine chronologies and climate indicated that precipitation might be this factor of influence. The strength of the chronologies' statistics (rbar, mean sensitivity, EPS) also reinforces the influence of abiotic condition on tree growth.

5. Conclusions

To the knowledge of the authors, this study is the first to deal with the tree-ring analysis of species from xerophytic thickets of Madagascar. It demonstrates the possibility to crossdate Malagasy species and to develop dendrochronological series from these data. It also concludes that the studied species are growing slowly and need several years to reach the minimum cutting diameter. The accuracy of ring measurement and correlation with external factors (precipitation and SST of ENSO regions) for the determination of tree ages varies among species, depending on ring distinctness and its regularity of formation. However, a larger number of samples and more information on species phenology would increase result accuracy to derive long paleoclimatic chronologies. Dendrochronology will hold a tremendous function on estimating productivity, annual aboveground biomass and more importantly on providing long-term series that have great potential for climate reconstructions of Malagasy forest species, leading to more effective and sustainable development.

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